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Research Article

Darwin and Lotka:
Two concepts of population

Philip Kreager

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Philip Kreager [1]

Abstract

Population was the subject of two major conceptual developments in the second quarter of the 20th century. Both were inspired by evolutionary biology. Lotka developed a mathematics of evolution in human and other species by analogy to thermodynamic models. His theory followed demographic practice in treating populations as closed units, commonly macro-scale, and in inferring underlying processes of change from aggregate outcomes. In contrast, the evolutionary synthesis – a collaborative product of research in experimental and population genetics, natural history, and related fields of biology – followed Darwin in insisting that close observation of small-scale population processes and local environments is necessary to understand population change. Because gene-environment interactions rely on expanding and contracting networks of individuals, the populations in question are by nature open. Despite the apparent conflict between these positions, the synthesis broke new ground in the history of population thought by showing how the two approaches could be combined. Demography, however, moved away from evolutionary and population biology as a source of theory in the early post-war era, and this conceptual redevelopment of population was scarcely remarked upon. More recently, the tremendous development of genetics has recalled demographers' attention to evolutionary theory as an inescapable element of modern population thought. This paper provides a historical introduction to mid-20th-century developments in Darwinian population thinking, and the implications of its dual conceptualisation of population for demography. Its potential importance extends beyond the problem of gene-environment interactions to many aspects of social network analysis.

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1. Introduction

The theory of population proposed in Lotka's two main works was formulated as a contribution to evolutionary biology. The *Elements of Physical Biology* (1925) elaborated a general mechanics of evolution in which relations between species are modelled as isolated systems obeying laws analogous to thermodynamics. This was reiterated in Part One of the *Théorie analytique des associations biologiques* (1934), and human populations were then treated as a special case in Part Two (1939). The period in which Lotka was writing was one of tremendous ferment in biology. The major contemporary breakthrough, which has come to be known as the "evolutionary synthesis" (Mayr and Provine 1998), was, however, formulated in terms that contrasted sharply to Lotka's. It addressed the dynamics of *intra*-species variation (Dobzhansky 1937). This focus, emphasizing relationships between individuals making up distinctive sub-populations, rather than species as undifferentiated wholes, was to have a lasting impact on the utility and reception of Lotka's work as a general theory of population for evolutionary biology. Lotka's method acquired an eminent role only in a sub-field of population ecology, the study of predator-prey relations, where it parallels work by Volterra (Scudo and Ziegler 1978; Kingsland 1985). This marginalisation is reflected in histories of evolutionary theory, in which the reader looks in vain even for mention of Lotka's two works (e.g. Provine 1971; Mayr 1982; Gould 2002).

Lotka's fate as a theorist of population evolution has not troubled demographers, assuming they are aware of it. His papers on American demographics (e.g., 1925 [with L.I. Dublin], 1936) established his pre-eminence in the mathematics of human populations, and no effort was made to translate the *Théorie* for almost half a century after his death (Lotka 1998). The argument that Lotka formulated the core of demographic theory was consolidated in a series of influential syntheses in the early post-war era: a magisterial survey of the social scientific domain of population research by Hauser and Duncan (1959: 1-117); Ryder's elegant sociological generalisation of Lotka's concept of population, taking account of subsequent developments in cohort analysis (1964); and a summary of the development of modern population thought (Lorimer 1959). The reconfiguration of Lotka's approach belonged to a disciplinary realignment that located demography firmly in the social sciences, while privileging its formal mathematics. The latter underscored the scientific status of the discipline, which Hauser, Lorimer, and Ryder considered in need of clarification and defence. The former refuted the accusation that demography is mere "macrobiometry" (Ryder 1964: 447), and distanced it from its recent association with eugenics. The impetus that Darwin had provided Lotka as a motive and foundation for his theory was quietly dropped.[2]

Evolutionary biology, of course, re-emerged in the 1990s as a potential source of evidence and theoretical insight into central demographic problems. Bio-demographers were quick to see that later stages of demographic transition (characterised by ageing, sustained low fertility, and epidemiological and dietary sequelae of modernisation) carry implications for the transmission of genetic material. Genetic factors, in turn, have potentially important bearing on demographic variables like increased life expectation, since current trends may in part be consequences of past adaptations shaping the human genome. Demography, in short, is integral to gene-environment interactions. This renewed interest in the fit between genes, organisms, and environments is of further interest because it has moved demography unavoidably toward issues of the kinds raised by Dobzhansky and the evolutionary synthesis. Thus, when Wachter writes:

> *experiments with laboratory organisms, genetic mapping, natural history, and evolutionary theory are defining the intellectual landscape within which demographic arguments and forecasts gain or lose their appeal (Wachter 1997: 2)*

he reiterates components that defined the evolutionary synthesis as

> *the fusion of three equally robust disciplines – experimental genetics, population genetics, and studies of natural history (Gould 2002: 531).*

This background to Wachter's observation, however, is likely to be unfamiliar to many demographers – a consequence of the shift away from population biology that demography experienced half a century ago.

The evolutionary synthesis has not featured in recent paradigmatic statements on evolutionary and bio-demography (e.g., Vaupel 2003, Kaplan and Gurven 2008; Wachter 2008). This is understandable: the synthesis, over half a century after its

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[2] While evolutionary and population biology was not explicitly rejected in these influential statements, its potential interest as a source of theory and method for demography was not explored. For example, of the 28 chapters that follow Hauser and Duncans' wide-ranging survey of the field of population research, only three (on genetics, physical anthropology, and ecology) were by authors concerned principally with developments in biology. In their extended discussion of demography's theoretical options (pp. 80-102), Hauser and Duncan merely allude to these chapters as addressed to fields that "overlap" with population studies (i.e., employ measures of a demographic kind). No major conceptual developments in population genetics or evolutionary theory are discussed. The chapter on genetics (Kallman and Rainer 1959), while giving examples that might be used to illustrate Darwinian population thinking, leads instead to a topic that helps us to understand Hauser and Duncan's reticence: links between demography and population biology were seen principally in terms of eugenics.

emergence, is a stage in the development of evolutionary theory with achievements largely assumed in recent developments. By showing how experimental, natural historical, and mathematical evidence reinforced each other, the synthesis resolved longstanding debates over mechanisms of natural selection that cleared the way for molecular approaches in our era. With time, growing knowledge at the microscopic and intracellular level has, of course, raised increasing questions at the environmental level of individuals and populations. Demography, with its emphasis on the many factors in a society that combine to shape mating, procreation, and death, is obviously integral to this environment. The emergence of evolutionary and biodemography was effectively predicated in the work of Dobzhansky.

Two fundamental features of the synthesis that extend beyond issues specific to the study of natural selection are likely to be of interest to mainstream demographers. The first is its articulation of the crucial role of intra-population dynamics – the role of networks as mechanisms that renew population heterogeneity -- in explaining population change. As Wilson and Oeppen remark, measures of variation developed by evolutionary biologists provide a recognised alternative model to demography's "tendency to look for single numbers to summarize complex phenomena" (2003: 126). The second feature is that, although Lotka appears to have been marginalized at the time of the synthesis, major players like Fisher, Wright, and Haldane drew on fertility and life table techniques, sampling, and other methods of a basically demographic kind. The synthesis, in short, brought the two conceptual approaches to population represented by Darwin and Lotka into a working relationship in which each applies to different parts of the puzzle of population change as appropriate to its own methodology and assumptions. The current re-emergence of evolutionary biology as a fundamental source of ideas and models for demography is thus important not only for opening up topics on the biosocial boundary, but as the locus of a general and fruitful conceptual framework in the study of population.

The purposes of this paper are threefold: to provide demographers with a brief historical summary of the two mid-20th-century conceptual developments of population and their relation to each other, to consider how these two modes of population thinking were combined in the evolutionary synthesis, and to call attention to this combined approach as a general model of population thinking. Although developed for research on gene-environment interactions, population thinking in the synthesis provides an example that appears to be applicable wherever purely formal and quantitative techniques need to be combined with what would now be called network population thinking. The importance now attached to conceptualising and measuring network processes as mechanisms of population change is evident in several mainline demographic topics, of which transmission of HIV-AIDS (Bühler and Kohler 2003), diffusion of contraceptive practices (Kohler and Bühler 2001), intergenerational transfers (Wachter 1997), and migration (Morris 2004), are examples. Open or Darwinian population thinking is important as a theoretical framework that can help demographers to clarify key relationships requiring explanation, and the methods appropriate to them.

The story begins with Lotka's theory and its sources, which are considered first and very briefly since they are more familiar to a demographic audience. Marked differences between his logic and the role of population in natural selection are then demonstrated in two ways: by noting how Darwin's development of Malthus differs from Lotka's, and from demography in general; and by reviewing the scepticism of some major contributors to the evolutionary synthesis, notably Ernst Mayr, regarding the capacity of conventional demographic methods ever to identify and explain processes of population change. The third section then draws out the complementary relationship between the two concepts as it emerged in the practice of the evolutionary synthesis. While Gould's "robust disciplines" continued to debate their respective roles in evolutionary theory (Mayr and Provine 1998; Lewontin 2001), there can be no doubt that the synthesis comprises a major chapter in the history of population thought. That analogous theoretical and methodological issues arise in Darwinian population thinking and current network demography is no accident. Darwin's conceptualisation of natural selection shares with demography common roots in natural history (Mayr 1982; Kreager 2008) and political economy (Schweber 1980, 1985). Examples of this re-emerging common ground are noted in Section Four.

2. Lotka, Darwin, and Malthus

Merely from the title of Lotka's *Elements* it is evident that, in his view, evolutionary biology does not stand alone. Reflecting his training in physical chemistry, he approached evolutionary theory by analogy to thermodynamics. Populations of species behave in certain critical features like populations of molecules (1925: 30-40; 1998: 16-20). The evolution of two gases, when introduced into a closed container, is characterised as a process of diffusion: the gases, previously separate in their own equilibria, when allowed to mix, obtain a new equilibrium having its own mass and other characteristics. The analogous task of population biology is to track the physical properties of species as they interact with each other. Relations between two species, say, a predator and its prey, should be analysed as material aggregates in evolution toward characteristic equilibria. Although laboratory conditions are needed to treat actual populations of molecules as closed systems, the analogy assumes that the model can be transferred directly to species in the field. Lotka's application to human populations thus begins by affirming the "very natural abstraction" of a closed population (1998: 53). The physical chemistry method, as Lotka calls it (1925: 41) can be traced to his earliest demographic analysis, in which molecular stability and life table functions are treated analogously (Lotka 1907).

Lotka never parted from his view that the theoretical framework to which demographic analysis belongs is evolutionary biology. In introducing their translation of the *Théorie,* Smith and Rossert note that he was working on an English edition at the end of his life, and that he had intended to add a third volume that would include more materials from the *Elements* (1998: xvii). Lotka did, however, begin to modify the framework in ways that remain incomplete. In the second part of the *Théorie,* he abandoned his emphasis on species interaction, arguing that human populations are a special case that can be developed in isolation. Culture has given rise to institutions unique to humanity (he cites monogamy and prolonged adolescence) and to patterns of population growth independent of relations with other species (1998: 42-47).[3] Although the predator-prey model is obviously too simple to account for the influence of the social and economic environment on human reproduction, Lotka did not indicate how this environment should be modelled for the purposes of his evolutionary theory. Presumably, relations between the human and animal parts of his evolutionary framework would have been clarified had he completed his revision of the *Théorie,* although it is difficult to see how this could have been done.

As a general framework for evolutionary biology, Lotka's formulation was ambitious, addressing a central issue – fertility as a mechanism of survival -- in the theory of natural selection. Darwin's source of Malthus for the idea of the survival of the fittest introduces Part One of the *Théorie* (1934: 3). For Lotka, as for Darwin, the number of individuals that compose a mating population, and their ability to sustain equilibrium, are important indicators of evolutionary success. However, as Mayr (1982: 477-494) remarks, the famous passage in Darwin's notebooks in which he described how his theory was stimulated by reading Malthus refers only to one aspect of natural selection. Darwin drew from Malthus the insight that superfecundity is a crucial locus in the struggle for existence: if natural selection acts on individual offspring, only some of which survive, then mortality will shape the pool of inherited traits, and individuals with greater numbers of surviving offspring have an advantage in passing their traits to future generations. In developing this point, however, Darwin diverged fundamentally from Malthus and the "very natural abstraction" of a closed population. As Darwin is

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[3] Subsequent research has not supported these premises. Life mating pairs in other species are well documented (Alcock 2001); Lotka's reference to 'adolescence' has been superceded by studies of adaptation over animal life courses (Daan and Tinbergen 1997); and his reference to species 'independence' over-simplifies the realities of niche construction (Odling-Smee et al. 2003).

often said simply to have followed Malthus's lead, it is worth drawing out this contrast in some detail.

Malthus, as is well known, saw aggregate factors like the demand for labour as constraints that ultimately shape all individuals' behaviour. He hoped that by education and severe limits on the public relief given to labourers it would be possible to encourage social and economic adaptations, which he understood in the limited sense of deferred childbearing and celibacy, which would keep the supply of labour from greatly exceeding demand, thus checking population growth (Wrigley 1987). He was, however, famously pessimistic: society and economy would always be vulnerable to the failure of many, and possibly most, labourers to adapt in this way (Malthus 1890: 456). The children of poor, out-of-work people are inevitably at risk, and their mortality then becomes a major check on the recruitment of new generations. In this approach, all individuals can be treated as essentially the same, since they face the identical problem of reproductive prudence.

People do, of course, respond differently to economic constraints, and variations in the growth and size of populations are composite outcomes of the choices divers individuals and groups within a society make. Malthus was nonetheless emphatic that, whatever these variations, populations must be considered as closed entities defined by the material reality that confronts all individuals: the famous 'principle of population'. The fixed limits of agricultural growth (confined permanently within arithmetical rates of increase), in relation to the capacity of human superfecundity (i.e., geometric population growth), make any other approach in his view unrealistic (1890: 460, 567). Relations between populations, for example via migration, are no solution, since they only postpone the problem (1890: 324-32). Wishing to improve people's adaptive behaviour, Malthus focussed on how macro-level implications of political economy should inform policies to constrain reproduction. He did not pursue his analysis at lower levels of aggregation, except in terms of idealised and stereotyped individual and family choices. The extent to which differing rates of fertility and mortality may be conditioned by relations between distinctive sub-groups (e.g., socio-economic strata, religious and cultural identities) and shaped by differing institutional networks (e.g., diverse family systems, migration streams, inheritance practices, institutions of civil society) have thus remained open and perennially controversial questions with respect to his theory.

Darwinian natural selection, in contrast, locates the primary agency of change at the level of individual interactions in relatively small communities; neither the course of change nor the relative importance of competing causes can normally be established directly from the macro-level without prior observation and analysis of local phenomena (Lewontin 2001). The uniqueness of each individual and of his or her mating and other networks are, from this perspective, key dynamic factors: species evolve because genetic diversity enables certain members, on the basis of inherited traits, to cope more successfully with the environment and to pass these (and other) traits to future generations, whilst other individuals die out. Heterogeneity arises not just from genetic variation, but from behaviour (e.g.. competition and adaptation) in which differing environments provide conditions that interact with inherited traits to establish differential adaptive capacity. A population, in other words, is not by nature closed but open, its membership changing through a continuous interplay of random genetic and selective adaptational processes.[4] A species at a given point in time will be composed of several sub-populations (demes) having variant features (e.g., polymorphisms) each created by its own networks of sex and related behaviour. In consequence, the word 'population', for purposes of natural history, experimental and population genetics, commonly refers not to an entire species population, but to groups within which individuals look for mating partners (i.e., Mendelian populations). Darwin's emphasis on processes that renew population variation, as opposed to treating populations as closed types or classes, has come to be regarded as "the foundation of his theory and his most revolutionary contribution to biology" (Futuyma 1986: 7).

As the implications of the evolutionary synthesis were gradually articulated, one of its principal architects, Ernst Mayr, drew a radical contrast between Darwin's reasoning and what he called "essentialist" or "typological" approaches, i.e. the long demographic tradition from Graunt through Quetelet to the present day (1976: 26; 1982: 45-47). His point may be seen clearly with reference not only to Malthus, but to everything entailed by the familiar 'demographic equation'. As is well known, demographers treat populations as units closed at a given point in time *t*, in which all individuals are typified by a limited set of indispensable or essential attributes (age, sex, marital status, and so forth); population change at any subsequent time *t+1* is, then, an alteration of the original population (e.g. more or fewer people of each age, sex, etc). In contrast, Darwin's emphasis on the distinctiveness of individual members of a population, and on mating and other relationships between these individuals, was designed to capture the emergence and spread of new kinds of individuals and characteristics as they may give rise to sub-populations distinctive from the original one, and potentially to new species. A population defined only as a closed set of types and attributes clearly cannot account for such changes without additional information.

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[4] Obviously Darwin wrote before the terminology of experimental and population genetics became customary. Here I follow historians' custom of using recent terms like 'gene' where they are consistent with Darwin's reasoning. 'Darwinian population thinking' is Mayr's (1982) phrase for the whole approach described in this paragraph.

2.1 Discussion

Mayr's clarification, in other words, was a signal reminder that Darwin's phrase 'origin of species' is a statement about population dynamics. The contrast between Lotka's and Darwin's approaches may be summarised in three main points, each of which has a crucial role in explaining how and why population change occurs. The first is the scale at which primary population changes take place. As we have seen, Lotka and Malthus give primary importance to analysis at higher levels of aggregation. The individuals composing a given aggregate are taken to be homogeneous, and the importance of local-level variation is discounted, so that phenomena at micro- and macro-levels are treated as if they were considered homologous. Darwinian population thinking, in contrast, focuses first on individuals and relationships among sets of individuals at local levels in order to track environmental and genetic outcomes of particular networks.

The second difference lies in how populations are constructed. For demography, each individual, once born, may vary only by quantitative changes in formal parameters (e.g., age, residence, parity, etc.) specified in the initial definition of the population as a closed entity. Principal units of population are often given by administrative or methodological conventions (e.g., censuses, registration districts, random samples). As Harrison and Boyce remark, "demography essentially provides a methodology which can meaningfully be applied to many situations which are not primarily concerned with population definition" (1972: 3). In contrast, the processes by which populations come to be constituted are a primary object of evolutionary research. Intra-population changes, such as mating networks and niche construction, have the capacity to expand or contract over time, leading to differing dispersions of characteristics within a species, new sub-populations, and even new species. Debate has continued over the relative roles and importance of the several processes (mutation, genetic drift, and environmental adaptation) that effect natural selection, but it is clear that these issues can ultimately be resolved only in terms of how local reproductive groups expand or contract over time. Of course, once a network population, such as one defined by mating patterns, is established, then demographic and population genetic models based on sampling may be applied – a point to which we shall return below.

The third contrast concerns the renewal of population memberships. Lotka's formal mathematics is now known as 'renewal theory' (Tuljapurkar 2002), which addresses how a population *as a whole* is renewed via fertility and mortality. Darwin's focus, however, was also on *the renewal of population variation* -- a concern that arises precisely because of limitations in the Malthusian account. Malthus, as noted, was concerned that certain forms of human behaviour are maladaptive and tend to increase mortality; in Darwin's theory, differential mortality functions similarly as a mechanism of natural selection that tends to remove less competitive individuals. If, however, mortality was truly the only check on less adaptive characteristics, and populations were actually closed to relations with other populations and to internal sources of variation, then the range of available characteristics would continually lessen, as mortality eliminated more and more genetic material. This situation obviously cannot be the case, given the continuing diversity observed within species populations. Hence the critical importance of recognising that populations are open, i.e., defined by network behaviour not bounded by any fixed group. Relationships *between* individuals are key to population dynamics because their structure reveals how individuals with differing characteristics are brought into association in differing or changing environments, and with what consequences. Individuals and groups with unanticipated characteristics may emerge either internally (from the capacity of mating and other network behaviour within a population to generate continuing variation) or externally (from traits acquired via networks that include members of other populations).

A familiar example is sufficient to show the potential importance for demography of Darwin's emphasis on the renewal of population variation. The central pattern of modern population change, the demographic transition, was conceived initially as a universal move toward stable low fertility and mortality (Notestein 1945). Subsequent research has, to the contrary, documented a remarkable diversity of transitions (Coale and Watkins 1986; Chesnais 1992), the likely importance of network (e.g., diffusion) behaviour as a mechanism within and between populations (Watkins 1987), and the continuing heterogeneity of post-transition settings, even within a narrower range of total fertility (Kuijsten 1996). An explanatory framework that accounts for this seemingly relentless renewal of heterogeneity in transitional and post-transitional behaviour remains an outstanding, and central, conundrum.

3. Relating the two concepts

To this point, discussion has focussed on path-breaking developments of population in the middle decades of the 20th century. For heuristic purposes, a shorthand phrasing – 'open' versus 'closed' population thinking – has been used to help summarise their major differences. The respective approaches may also be contrasted as basically 'bottom-up' (i.e., beginning from local networks in small scale populations and moving toward higher level changes, such as speciation) and 'top-down (analysis in which local processes are inferred from aggregate structures and trends). Both concepts played crucial roles in the evolutionary synthesis, and it is to their relationship that we now turn.

Are there lessons for demography in the way evolutionary biologists brought together the two concepts? How successful was this integration? Can currently topical issues in demography that require us to observe network behaviour and track their diverse aggregate outcomes – family support systems, contraceptive diffusion, sexual networking, transmigration – be informed by the conceptual and methodological accommodation of the two concepts achieved in evolutionary theory?

Discussion at this point moves beyond the contrast between Lotka's theory and the synthesis to debates between Gould's "robust disciplines." While successful in reconciling Darwin's account of natural selection with Mendel's research, evolutionary biologists of the 1920s and 1930s often failed to agree on the status of the two concepts. As we shall see, the concepts played complementary roles in the synthesis; while both are integral to understanding population change, they remain conceptually distinct. Clarification of their complementary nature nonetheless remains one of the major achievements of the synthesis. The concluding section of this paper gives some analogous examples in current demographic research.

3.1 The two concepts in the evolutionary synthesis

The period from 1907 to 1939, when Lotka's ideas were taking shape, was an era of sustained disagreement amongst evolutionary biologists in which the central importance of Darwin's distinctive approach to population was gradually clarified. Over much of this period, for example, a substantial body of scientific opinion believed that Mendel's researches disproved rather than supported Darwin's account of natural selection. The first critical steps in the synthesis are generally attributed to Fisher (1930) and Dobzhansky (1937). Looking back on debates of the period, Lewontin observed that "the perceptions of those engaged in the synthesis differed significantly from the actual state of knowledge that existed on the theoretical plane" (1998: 58). In practice, evolutionary biology employed both concepts of population, but individual scientists differed adamantly in their views of them.[5]

On one hand, there can be no doubt that sampling procedures enabling populations to be constituted as closed data sets, and models developed in relation to them, played a crucial role in the synthesis. Data derived from controlled laboratory populations enabled experimental geneticists to explore gene mutations, and structural and numerical chromosome changes, as principal sources of variation. Probably the best-

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[5] In this and following sections I follow historical accounts (Provine 1971; Mayr 1982, 2004; Mayr and Provine 1998; Gould 2002), in which the many competing arguments are grouped into two strands. This may at first appear to suggest that all that is at issue is an opposition between natural historians and population geneticists. Experimental genetics, however, drew on both approaches, and major mathematical geneticists, like Wright, contributed to the design of field studies.

known examples are the "fly lab" studies of anatomical specialisation in *drosophila* carried out by Morgan and his associates (Mayr 1982: 752ff). Experimentalists, in employing formal mathematical approaches, parted from Darwin's methods not only because this enabled more rigorous comparison, but because this enabled them to capitalise on advances in other aspects of biological research, such as cytology and microscopy. It also enabled correction of errors in Darwin's theory, notably his acceptance of 'soft' and 'blending' inheritance as possible mechanisms of evolutionary change.[6] Population genetics was able to move beyond simple relative frequencies to address technical issues involved in sampling, and to explore a range of possible models. These included thermodynamics, which Fisher, whose role in combining conventional demographic and new genetic measures was pre-eminent, rejected.[7] Initially, experimental approaches saw genetic change in a given population as driven by mutation rather than by natural selection, evolution proceeding discontinuously via jumps, rather than small steps as Darwin had stressed. A substantial body of criticism, from Bateson and early interpretations of Mendel up to the 1920s, favoured abrupt mutational changes ('saltation') as the basis of new species, despite emerging experimental evidence to the contrary.

On the other hand, genetic results based on laboratory research were recognised to provide an incomplete picture of conditions in the natural world, a point with which proponents of mathematical modelling, notably Fisher, Haldane, and Wright, all concurred (Provine 2003: 66). Some advantages of natural observation could be adapted

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[6] 'Soft inheritance' refers to the idea that characteristics shaped, for example, by climate or nutrition in an individual's lifetime, might be inherited. 'Blending inheritance' is the idea that offspring inherit an average of parental characteristics.

[7] Lotka's idea that evolutionary theory and demographic analysis rest on analogies between biological processes and those of physical chemistry belonged to a common intellectual current of the late 19th and early 20th centuries. The second law of thermodynamics, which inspired the fundamental equation in Lotka's theory, was also explored by Fisher (1930), and recurs in biomathematical discussions of the era (e.g., Pearson 1900; Wright 1931). The problem of reductionism, *i.e.*, of tending to reduce biology to physics, put all but Lotka off such an approach. Fisher (1930), in taking the first step toward the evolutionary synthesis, was writing after Lotka had pointedly and publicly (1927) called his attention to the *Elements*. Yet Fisher made no reference to the latter's work in his *Theory,* alluding to the thermodynamic analogy briefly and dismissively (1930: 36-37). Nor do the *Elements* and the *Théorie* figure in major texts of the second stage of the synthesis (Dobzhansky 1937, Huxley 1942, Mayr 1942; Simpson 1944), which saw the integration of Fisher's *Theory* with developments in experimental genetics, systematics, ecology, and paleontology. Problems with the concept of population that Lotka employed were basic to wider rejection of the thermodynamic analogy. Lotka could adopt this analogy because, in his view, all members of a species, and all relevant environments, could be treated like so many molecules under laboratory conditions, *i.e.,* as identical for purposes of species competition. This, of course, was an immense simplification, as not all prey are equally vulnerable, nor predators equally efficient. Biologists, from Fisher to Gould (2002: 511-512), rejected the analogy precisely because individual differences, and their aptness for survival in a range of diverse environments, are together key components of the conceptual structure of Darwin's account of natural selection.

successfully and even improved in laboratory conditions. By focusing on species with short generation intervals, for example, it was possible to observe changes in particular traits directly and track them empirically for many generations. Other factors, notably the effective size of demes as units of genetic change and levels of migration between breeding populations – both necessary to construct the breeding structure of the population – could not be created in lab conditions. Here the evidence of natural history, employing methods familiar to Darwin, was critical. Population diversity observed in field conditions, taking account of ecological factors that effect geographical isolation of breeding groups, was clearly needed to identify mechanisms of natural selection. These results (Mayr 1942) contrasted sharply with those of early interpreters of Mendel: speciation proceeds continuously via the relative frequency of small genetic changes consequent on the differing adaptations of sub-populations in their respective niches. The need to unite experimentalist and naturalist approaches was recognised particularly by Dobzhansky and Wright, leading to the series of field studies published as *The Genetics of Natural Populations* (Lewontin et al. 2003). These and other studies begun in the 1930s showed considerable ingenuity in devising sample populations that provided evidence suitable for formal analysis, while nonetheless observing and capturing migration and mating processes characteristic of open populations.

In consequence, the evolutionary synthesis is usually described as achieved in two phases. First, Fisher (1930) used closed population models to demonstrate that gene frequencies revealed in experimental populations were in conformity with the naturalists' evidence that selection proceeds in continuous, small steps, rather than by abrupt mutations.[8] His model combined conventional life table analysis with tables of reproduction by age and genetic variation. These results brought an end to previously unresolved debates over soft and blending inheritance. A second problem, however, remained: How could a continuous process of genetic change yield discontinuities, i.e., separate demes and new species? This is, as we have seen, the critical point at which Darwinian population thinking diverges from Malthus's. The second phase of the synthesis, initiated by Dobzhansky (1937), noted that genetic variation is only part of explaining the origin of species: varying gene frequencies account for the diversity of building materials that can make up an individual, but are only part of how materials are combined in the building process. Many genetic variations are 'neutral'; that is, they play no part in adaptation. Thus to sort out which factors are critical to evolutionary

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[8] Later discussion of the evolutionary synthesis has reintroduced abrupt changes, not at the level of genetic mutations, but major environmental shifts, together with the criticism that with time the account of the synthesis (including several sources followed here) has been simplified to leave out other aspects of variation (Gould 2002).

change, it is necessary to place variation within the natural history of actual populations, so that genetic differences amongst individuals and demes making up a species are linked to their more or less successful adaptations under varying ecological conditions.

3.2 Discussion

As in post-war demography, a tendency can be observed in these debates to oppose arguments that emphasize populations documented by sustained qualitative and numerical observation in field conditions, to approaches emphasizing formal models and more extensive quantitative datasets.[9] Natural historians, paleontologists, and some experimental biologists, in taking the first line, argued that statistical modelling becomes critical only at certain points in the development of Darwin's theory. Geneticists trained in Fisher's methods, however, countered by arguing that the second phase of the synthesis merely documented and generalised the implications of mathematical genetics (Provine 1998: 51). The difficulty of recognising that the preferred population concepts of both approaches are necessary components of evolutionary theory underlies Lewontin's observation (cited above) that practice lagged behind theoretical development.[10] As a scientific breakthrough, the role of population in

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[9] The post-war demographic situation was reviewed, for example, by Hawthorn (1978: 6) in language that evokes biological parallels: "neo-classical models, both macro and micro, have shown themselves to be so rough and ready, so approximate, as to make one wonder whether they do not actually constitute a systematic distortion of facts and of the mechanisms which connect them. Perhaps the time has come for a change, if not for a complete collapse into natural histories…"

[10] There is not space here to consider other aspects of this extended debate, but Mayr's central contribution to the history of population thought deserves note. Briefly: on the naturalist's side, Mayr (1982: 45-47) was emphatic that population thinking refers only to processes that give rise to distinctive mating groups which may expand or contract in a given environment. A species consists of demes, populations that are not closed mating groups, and any account of its evolution must focus on the processes that tend to isolate these groups or bring them together. As noted above, he contrasted this way of conceptualising populations sharply to demographic traditions that treat populations as closed aggregates. Mayr's account, however, took for granted the role of sampling and Fisher's life table analyses. As the *Genetics of Natural Populations* (Lewontin et al. 2003) and other studies show, natural history leads at some stage to taking samples. That is, closed population methodologies are employed once the genetic and environmental processes that at least potentially link sub-populations have been identified. Of course, not all such hypothesized linkages are established. Tracking micro-level population changes, whether in natural or laboratory conditions, is an empirical procedure that may require the drawing of successive samples until a frame suitable to capture a given pattern of selection is identified.

Mayr, in other words, can be understood as making a point of principle: local dynamics of selection and adaptation in open populations are of fundamental importance *at the level of theory*, while sampling procedures and formal population models are technical devices that may be brought to bear in exploring genetic variance, and hence to documenting, developing, and generalising theory. His argument at base is that the synthesis is of evident wider interest for population studies: here we find the first general solution to how the two population concepts can be combined, providing examples of their respective roles at several levels of analysis. The complementary relationship of the two concepts may be summarised briefly, before turning to implications for demography.

On one hand, in the logic of Mendelian or intra-population change, groups in the natural world exchange genetic and other material via networks that favour certain members' reproduction and admit some external members. The capacity of group networks and environments to expand and contract means that these populations are open, and their openness is important because it leads not only to changes in population composition, but the evolution of species. In studying mating behaviour, and discovering differences and relations between sub-populations within a species, naturalists could often rely, for example, on observable features of organisms in combination with effective geographical isolation to define units of population, without reference to statistical samples. On the other hand, such isolation is not readily observable in most circumstances, and Dobzhansky and Wright showed how, once specific properties of breeding groups are understood sufficiently to formulate hypotheses, field samples could be taken for experimental purposes drawing on insights from mathematical population analysis. In other words, open populations must at some stage of quantitative description and analysis be treated as formally closed. Formal models, in turn, commonly lead to alternative hypotheses, at which point knowledge of the "small steps" effected by mating networks and natural selection in composing actual populations will be needed to test them. In evolutionary theory, with its strong emphasis on comparison of populations defined under actual as well as artificial conditions, both modes of population thinking have a part to play.

Undoubtedly, the easiest way of understanding the complementary character of the two modes of population thought is by employing the metaphor of *networks*. Mating and niche construction over generations produce networks of related individuals within

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Darwinian population thinking is the inescapable starting point: if population genetics ignored the exchange of genetic material between sub-populations, evolutionary processes could not be explained. That said, his pointed opposition of Darwinian to essentialist or demographic approaches clearly gave incomplete attention to the role of formal population analysis. Mayr later implicitly acknowledged this shortcoming (cf. Mayr 1982: 45-47 and Mayr 2004: 121-126).

Geneticists meanwhile were aware that few naturalists fully understood more than the outlines of Fisher's work. From this point of view, Dobzhansky's field studies were able to show genetic changes in sub-populations chiefly because they could be designed in ways that enabled evidence to be fitted to models. Dobzhansky was very frank about his dependence on mathematical advice in constructing his field samples (Provine 2003: 70). However, this argument, too, was incomplete. The mathematics of variation from Fisher to Wright was predicated on Darwin's conceptual framework – the logical structure in which superfecundity, variation, selection, and adaptation *together* form the mechanisms by which sub-populations exchange genetic material and evolve – which rests, of course, on Darwin's research and analysis as a natural historian.

which particular characteristics and evolutionary adaptations may be tracked. The populations built up from such networks change their evolutionary character as interactions of individuals continue – the processes and the populations are open, but not infinitely. Description and analysis inevitably work with populations at a given point or points in time. For this reason, open populations may be understood for research purposes as composed by and of *limited but unbounded networks*. Mathematical modelling then enables hypotheses about network diversity and their implications at local levels to be examined in larger samples and wider evolutionary theory.[11] The conceptual and substantive pay-off of an approach based on open *and* closed population analysis is evident in the subsequent course of evolutionary biology. The framework of the synthesis, by eliminating the false leads of saltation, blending, and soft inheritance, and by clarifying the respective roles of the several 'robust disciplines', cleared the way for post-war modelling at the molecular level, notably the work of Watson and Crick, and more recent molecular biology. In effect, a more efficient division of scientific labour was made possible, in which the use of models and samples to explore dispersion of genetic mechanisms at the molecular level presupposes that evidence from local observation of network outcomes in actual populations has been, or could be, identified.[12]

4. Demography and open population thinking

Analogies are powerful engines of scientific discovery (Canguilhem 1963; Hesse 1966). Their role at crucial transition points in the history of population thought is unmistakeable. Thus, the first quantitative population inquiry began in the threefold analogy Graunt (1662) made between: 1. methods of calculating relative balances in merchant bookkeeping, 2. Baconian natural history as a method of observing balances in nature, and 3. prevailing early modern ideals of balance in the body politic (Kreager 2005). Lotka's core analogy, as we have seen, was between evolving equilibria of species populations and of molecules. The role of mortality in Darwin's model of natural selection was an analogue of Malthus's principle of population. As the evolutionary synthesis showed, however, Darwinian population thinking also requires a

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[11] Fisher's *Theory* did this for gene frequencies, and measures based on Lotka's development of intrinsic growth rates could be applied to demes once they have been identified, much as the Volterra-Lotka equations used in predator/prey models are employed in population ecology.

[12] The realisation of this programme in population biology, however, remains incomplete since interaction between molecular phenomena and ecological and social variations can be explored in depth only after relationships at the molecular level are reasonably established (Singh and Uyenoyama 2004).

second concept of population, based on observation of evolving networks in local populations. Are there analogies that demography might draw from evolutionary biologists' pragmatic resolution of this duality in modern population thought?

The synthesis effectively rearticulated two issues: How one *defines* a population, and how the definition adopted should depend on the nature and level of the phenomena requiring measurement. Is a population any aggregate of individuals with certain characteristics, or is it an aggregate *composed by network behaviour,* i.e., in which individuals, small-scale aggregates, and their characteristics are defined by specific interactions observed between individuals and between changing sets or sub-populations of individuals over time? The latter definition carries a critical advantage: it goes beyond the issue of population renewal to address the renewal of population heterogeneity, the nature of the formation and successive internal differentiation of sub-populations. The result is a deeper and more empirical explanation of population change and of the nature of innovation.

Potential implications for demography of a theory of population embracing both aspects of renewal may be illustrated briefly. Two sorts of example are useful. The first is less an analogy than a continuation of evolutionary biologists' approach to gene-environment interactions. A case in point is biodemographers' interest in intergenerational transfers as a social system that may improve longevity. A second example is the growing body of network analysis of fertility change, which raises issues of heterogeneity analogous to those of evolutionary biology.

4.1 Biodemography and intergenerational transfers

A basic strategy of biodemography aims "to measure population-level allelic frequencies in human samples and examine their correlations with reported behaviours and social characteristics" (Wachter 2008: 1505). As Kaplan and Gurven (2008) note, this strategy is supposed to proceed in two directions: 'bottom-up' (i.e., from molecular level changes up to their population level consequences) and 'top-down' (i.e., beginning in theoretical implications of why natural selection at the aggregate or species level should favour certain changes over others).[13] Of course, the phenomena with which demography ordinarily deals lie at levels between proximate microscopic factors and ultimate evolutionary explanations, and are likely in many, if not in most, cases to be neutral in their evolutionary effects. An hypothesis put forward by Kaplan (1994) and Lee (1997) suggests an interesting area in which the issues raised by this strategy may

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[13] As noted at the beginning of Section Three, the 'bottom-up'/'top-down' imagery may be applied differently in studies of human populations, where the 'bottom' is the level of individuals and small groups.

be considered: downward transfers of wealth and support (i.e., from grandparents and parents to children), by improving the conditions and life opportunities of children, should over time increase the fitness of descendents, enabling the longevity of older generations gradually to improve. For example, children who receive transfers may, in the economists' jargon, be of higher 'quality', and thus more attractive as potential mates. This may, in turn, increase their chances of having children, the size of their social networks, and the likelihood of mating with partners from different sub-populations. Upward flows might also help to prolong elders' lives, but would be counter-effective in evolutionary terms if they seriously reduced food and other necessary support to the young. This hypothesis clearly originates in Kaplan and Gurvens' 'top-down' reasoning. Initially regarded as a particularly promising bridge between evolutionary biology and mainstream demography, it has more recently been described as facing serious problems (cf. Wachter 1997: 8 and 2008: 1506). Recognising the important role of both concepts of population in formulating this issue in both 'directions' helps us to understand what the difficulties are, and how the renewal of population heterogeneity is central to them.

Ideally, developing the hypothesis entails three major tasks, only some of which fall to demography. The first belongs squarely in the geneticists' domain: the need to identify alleles or portions of chromosomes that have specific effects on the physiology of ageing. The second would unite genetics and demography, as it brings together the study of local networks and the development of appropriate survey and sampling methods: the need to track Mendelian populations (i.e., those sharing relevant alleles) in relation to sub-populations of kin and others who comprise support networks. According to the hypothesis, differential participation in wealth flows over many generations should influence significantly the demes or sub-populations in which alleles are distributed. Some networks will provide more support than others, and the longevity and other demographic characteristics of sub-populations created by these networks may then be compared to the spread of longevity-enhancing alleles. Environmental factors – e.g., changes in state infrastructure and support – obviously need to be taken into account, since they may provide alternatives to intergenerational support. The understanding of network or open population behaviour gained in local populations in the second task informs hypotheses in the third: the design of samples of wider populations, including biomarkers. If genetic data are to be translated, for example, into a form useful for public health policy, likely characteristics of those sub-populations in which longevity is positively or negatively affected by the interaction of wealth flows and genetic features will need to be identified.

In his review of evidence on inter-generational wealth flows, Lee focuses on the third task, arguing that the "interest is the broad pattern of flows, on average, in a population" (1997: 220). Beginning with the third task is at present dictated by available demographic evidence. Intra-population differences in wealth flow behaviour are not extensively studied, so that the second task has to be taken as given. What are the implications of this shortcut? It requires us to assume that local variations in flows of wealth and support are without important evolutionary impacts – an assumption which possibly runs against Darwin's account of natural selection, in which local network heterogeneity is a key force in population change. As recent reviews note (e.g., Lee 1997; Kaplan 1994; Kaplan and Gurven 2008; Kreager and Schröder-Butterfill 2008), extant research on wealth flows is highly selective of the types, duration, and extensiveness of exchanges that get reported. This raises potentially serious problems, since it is far from clear that key sources of variation are monitored sufficiently to carry out the research strategy. Problems noted in the several reviews include the following: many studies refer only to some aspects of support (e.g., food or labour); informants may not report income and exchanges accurately for various reasons, and different members of a network may give differing reports of the same exchanges; the scale and directionality of flows are distributed differently across the life course, yet most studies are of limited duration; since many forms of support are not monetised, standard measures for comparing different forms of support (e.g., services versus food) have proven difficult to establish; bequests tend to be treated separately from daily support provision, although in some societies the former take place gradually over the later life course in response to specific needs in the younger generation; usually only benefits, and not the costs, of transfers are considered; studies tend to focus on a single community or survey, in which the population is taken as homogeneous; and research may focus on transfers within households, even though support in many cases relies on networks of households, including those outside the community.

Several of these limitations are analogous to those raised by Mayr and others in the evolutionary synthesis. For example, the last limitation – whether the role of non-resident kin is accurately included – raises the question of what defines the boundaries of the population and sub-populations under analysis. Human network populations need not be continuously resident in the same place, and the mating and transfer behaviour of non-residents may be incompletely recorded without careful further inquiries. Population network boundaries within a community, and the changing memberships they describe, are likewise critical. What is the range and relative importance of kin involved in transfers between generations?‘ How is the quality and quantity of support structured by local hierarchies and patronage networks? Do the rich help their poor kin? To answer these questions, knowledge of institutional networks beyond those of mating and transfers is likely to be necessary. Data on these and related questions normally require evidence from sustained ethnographic observation, which can then be backed up by representative local samples designed to capture network characteristics. Other limitations mentioned above concern tracking the heterogeneity of content, scale, and duration of flows, which are important in specifying sub-populations that may be behaving in significantly different ways over time. Some studies show that the directionality of flows is not uniform (i.e., flows pass both 'up' and 'down' in different parts of a community at the same point in time); changes in the direction of flows can vary radically over individual life courses, and an equality of support may exist in long phases of family life cycles.

Observation of network processes that include these variations takes us directly to the key evolutionary issue of adaptation to environments. Support flows normally adjust over time, a reflection of changing and competing needs of different members of a network. This flexibility is an important aspect of the role of networks as welfare systems. The continuing renewal of variation in flows, in other words, is a normative feature of a network's ability to adapt successfully so that it sustains and renews its membership. Levels, content, and directionality of flows may all vary in response to the balance of needs and abilities in different parts of a network. Evidence of flow heterogeneity is needed before we can assess whether average flows give an adequate picture of the potential evolutionary impact of wealth transfers. A further point of caution should be noted in relation to the identity of mating, as well as of support, networks: Are kin relationships as reported in surveys in fact reliable accounts of parenthood?[14]

In sum, the combination of open and closed population methodologies emphasized in the evolutionary synthesis appears to be no less important for addressing potential human gene-environment interactions than it is in other species. The evolutionary synthesis found that a combination of sustained observation of local networks and related behaviour, together with sampling, was necessary to identify the changing sub-populations that make up wider populations. Differences and relations between sub-populations, as well as relations with outsiders, continually introduce heterogeneity into networks, and into the wider population. In the absence of research which documents

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[14] Several of these points are illustrated by Indonesian data, although not collected with biodemographic issues in mind (Kreager and Schröder-Butterfill 2008). There it was found that accurate interpretation of survey data requires prior observation of network processes that define relevant sub-populations. Ethnographic methods enabled the study population to be treated as a set of open networks until the relevant sub-units could be established. Panel surveys based on random samples then compared three communities, finding that levels and the directionality of support flows were strongly structured in each by differences between sub-populations, notably socio-economic strata. Networks produced significantly different flows, variously 'upward', 'downward', and 'balanced', which varied not only between communities, but between sub-populations within them. Variations crucial to accurate recording of genetic differences, notably differing prevalence of adoption in specific sub-populations, also reflected strata and network features. Adoption, moreover, was often disguised, and could be identified only via sustained network observation (Schröder-Butterfill and Kreager 2005). These findings, of course, are subject to some of the 'selectivity' issues raised in the literature (e.g., our study of exchanges gives more weight to economic and food exchanges than visits and companionship).

the role of local processes in creating intra-population differences, the danger of reification, highlighted by Wilson and Oeppen (2003), is clear: a focus on average behaviour may confirm initial assumptions of homogeneity before sources and patterns of variation crucial to population change are even explored.

4.2 Social networks and fertility

In Darwinian population thinking, as we have seen, the renewal of populations depends on the renewal of population heterogeneity. A species is composed of sub-populations with varying characteristics whose differences give them differing adaptive advantages and disadvantages. Variation helps some sub-populations to survive unforeseeable changes in local environments, and to increase to a greater or lesser extent. In this broad perspective, the diversity of fertility transitions in human populations (Coale and Watkins 1986; Chesnais 1992), and the continuing variability of post-transitional fertility trends (Coleman 2007), are only to be expected. Although populations undergoing fertility declines may be subject to similar constraints, their differing history, together with variations in their current environments, give them differing capacities of response. Differing responses in turn carry the likelihood that varying adaptive capacities will continue to be introduced. Heterogeneity continues and is an integral component of population change.

However, over most of the later 20th century, demographic transition theory was predicated on a very different idea of population change, emphasizing the reduction of heterogeneity. Following Notestein (1945), all societies were supposed to converge on a stable low fertility, low mortality regime. The diversity of transitions revealed by the studies just cited embraces the timing, trend, and duration of demographic transitions, and uncertainty over the future of fertility in the context of current post-transitional variation. The assumption that heterogeneity is not a key issue has thus become impossible to sustain. The difficulty is compounded by the fact that these studies also show that trends in macro-social and economic variables, which were supposed to determine (or correlate regularly with) transition and post-transition in all societies, cannot explain so much variability. That a truly remarkable narrowing in the range of vital rates is occurring at a global level remains, of course, beyond question (Wilson 2001). Whether an adequate explanation of demographic transition and its consequences is possible without accounting for processes that sustain and apparently renew heterogeneity within this very broad convergence is, however, doubtful.

Demography’s increasing focus on social networks as key mechanisms of demographic transition – the diffusion of contraception, for example – emerged directly from this impasse (Kohler and Bühler 2001). Research on historical and contemporary populations showed that transitions occurred in adjacent groups, often sharing linguistic or other cultural characteristics, regardless of economic differences (Coale and Watkins 1986; Cleland and Wilson 1987). The implication is that fertility change is guided by variations in flows of information and practice within and between groups at various levels below the nation-state. Subsequent research has moved increasingly to include research and data on local populations and network processes that link them, and to use this to inform surveys and analysis (e.g., Watkins and Warriner 2003). From the perspective of evolutionary biology, the need for this shift in demographers' thinking is obvious: units and classifications used to track the transition are normally censuses and surveys, i.e., closed populations. Understanding heterogeneity and its renewal, however, requires a research strategy that does not take individual and population units as subject only to quantitative changes in fixed sets of attributes. The need is to identify processes by which individual characteristics and distinctive groups come to be constituted, and how and why their changing composition gives rise to new and previously unrecognised sub-populations. As we have seen, this approach emerged as a central focus of the evolutionary synthesis in order to study the way reproductive patterns are differentiated.

Demographers have, of course, often expressed concerns about the limitations of closed methodologies. For example, standard, and particularly governmental, sources commonly fail to include important sub-populations (e.g., data relating to parity, cause of death, ethnicity, resident aliens). The selectivity of official records, in recognising certain population groups and not others, can lead to a history of inclusion or exclusion of sub-populations that is bound up with past and present political agendas. To the extent that samples and surveys are drawn from, or are modelled on, categories used in public sources, they may perpetuate the problem. The difficulty of addressing integral population heterogeneity is thus closely bound up with issues of data content and quality. In this perspective, demography, like the evolutionary synthesis, faces a key issue of how to reconcile evidence and methods appropriate to two ways of conceptualising populations. The adequacy of extant closed population units and classifications can, however, be tested in a dual conception of population by examining the way networks, as open population structures, build up sub-populations characterised by different reproductive and other networks, and then looking at the extent to which important divergence in trends is disguised in conventional sources. The dual conceptualisation of population thus becomes a potential vehicle that demographers may use to make empirically based arguments for data improvements.

The study of diffusion has given practical impetus of this kind to several questions demographers ask. A good example is the emerging importance of 'selectivity', in which the need to control potential biases affecting population samples is viewed from the standpoint of how members of a network are implicitly or explicitly chosen by their fellows (Watkins and Warriner 2003). The importance of this issue arises in direct response to the limitations of closed population methodologies. Surveys in the developing world have for several decades shown a gap between people's contraceptive knowledge, attitudes, and actual practices (Westoff 1988; Casterline and Sinding 2000). The 'gap' is shaped by a potentially immense number of variables: differences in women's empowerment and roles in society, implications of the division of labour, differences of education. religious institutions, provision of health services, implications of different forms of contraception and their relation to other proximate determinants, and so forth. Within a given population, these several factors appear to come together to influence contraceptive practice in differing ways. People's retrospective reports of what they think and do as recorded in surveys do not study the process by which people learn and act, i.e., how knowledge, values and usage actually spread differentially in society. It is thus necessary to go below retrospective reports to explore how information, mutual support, gender, and related issues are structured by normative institutional and other networks.

The early spread of contraceptive use amongst individuals and groups, for example, is a process that builds on (or may be restricted by) existing ties between people, probably also entailing new links and changes in existing relationships. The set of people with whom contraception can be discussed will often depend in part or whole on extant local networks (amongst kin, workmates, generations, genders). Where the value and practicality of contraceptive use are of uncertain value, deciding who is an appropriate contact ("a person like myself", as a Kenyan woman told Watkins and Warriner 2003: 124) is likely to emerge gradually. The appropriate network, whether established or in the making, is a phenomenon that can be expected to expand or contract, as in Mendelian populations: the question of who belongs to a sub-population composed by networking cannot be taken as given in advance, and its changing size, composition and structure are demographic phenomena to be explored at the heart of social, cultural, and economic change. Variation in network membership, by introducing different individuals, characteristics, and a new range of links to potential others, may subtly or powerfully change network impacts.

Attempts to construct a general theory of diffusion in the social sciences began in the late 19th century, and by the 1970s, applied fields like technology transfer produced trenchant critiques that showed why diffusion theory remains unable to resolve several central problems (Kreager 1998: 298-303). Four of these problems persist in Kohler and Bühler's list of current criticisms of social network studies of fertility: ambiguity in the definition of what diffuses, reliance on indirect evidence, insufficient knowledge of the contexts that condition diffusion, and uncertainty over how and whether diffusion is a process that can be fitted to standard economic models (2002). As the authors note, however, network research, by moving beyond individualistic models of choice, provides some useful hypotheses. Differences in network structure, for example, may be used to describe separable processes of social learning (e.g., about new information and techniques) and social influence (the extent to which new knowledge and practice are accommodated by social norms) (Kohler, Behrman, and Watkins 2001). Conversation networks that shape contraceptive choices overlap with, and are drawn from, a number of existing networks at the local level (e.g., of kin, gender, labour, wealth flows); the functions and dynamics of these networks are likely to be important for understanding whether and how conversation networks on particular topics emerge (Weinreb 2004). Put another way, the dynamics of fertility change comes down to observable relations between a number of co-extant and overlapping sub-populations as defined by the networks that constitute them. Social network theory provides a number of further hypotheses here. For example, because local networks overlap and may reinforce each other, their conjunction may produce ‘multiplier effects’ that increase the spread of contraception; and differing levels of contraceptive use in sub-populations defined by different networks may form ‘multiple equilibria’ co-existent in the general population (Kohler and Bühler 2001).

As in open or Darwinian population thinking, this interest in local network phenomena reflects a need to develop concepts and methods that help us to understand heterogeneity. The role of natural historical observation in evolutionary biology, in providing qualitative and quantitative evidence of local processes, is taken in demography by ethnography and semi-structured interviewing. Local level data shape and help to test hypotheses arising from more general transition and social network theory, signalling a potentially healthy interaction between ‘bottom-up’ and ‘top-down’ approaches. A major difference, however, should be noted. A key role of natural history is to track and compare actual networks, and to delineate the sub-populations formed by them. In diffusion research, in contrast, observation and documentation of sub-populations units and how they change is not a primary objective; local knowledge may be sought chiefly to help identify variables that can be used in wider surveys. This shortcut is similar to that noted in wealth flow research (Section 4.1). Yet the four persistent defects in diffusion theory cited by Kohler and Bühler all point to the need for a deeper understanding and direct evidence: How are knowledge and practice altered when they diffuse between sub-populations? Can we say that the take-up of contraceptives is ‘innovation’ if it is an instance of adaptations that extant networks normally exist to carry out? Do models of economic rationality adequately capture these processes of population change? The implication of Darwinian population thinking for social networks and fertility is that observing and monitoring processes by which network populations expand and contract cannot be left out.[15]

5. Concluding note: Demography in the human sciences

This paper has addressed a major chapter in the history of population thought and explored some of its implications for current issues in demography. One of the striking features of demography's post-war reconfiguration as a social science was that population came to be defined in the singular: *the* concept of a population (Ryder 1964; Vance 1959: 295; Hauser and Duncan 1959: 38). With the benefit of hindsight, we can see that not one but two innovative concepts of population animated the 20th century – one in biology, associated with Darwin, and the other, in demography, with Lotka. The two concepts begin in fundamentally different research strategies, one addressed to processes that explain local population variation and its renewal, and the other to modelling aggregate population structures that are outcomes of these processes. Understanding processes of population change requires a balance between both approaches in the study of animal and plant species, and we may expect that human populations are unlikely to prove to be any different.

When demography turned away from evolutionary biology as a mainline source of theory in the early post-war era, it short-circuited its own awareness of scientific developments that, to echo Wachter, have come to define the intellectual landscape in which the subject now finds itself. Key issues, like the renewal of population heterogeneity, cannot be straight-jacketed solely into the social or the biological sciences. As suggested here, they belong equally to the study of transitional and post-transitional demographic behaviour and to wider processes of natural selection. The renewal of heterogeneity has, however, proven to be more readily accessible to conceptualisation and explanation in evolutionary biology than in demography. The reasons for this owe to the dual concept of population in Darwin's theory, and its clarification in the evolutionary synthesis. The co-existence of two orientations in the study of population (one concerned principally with the nature and cohesion of changing memberships, and the other with finite aggregates) did not begin with Darwin; it is a basic intellectual resource in European scientific and political thought (Kreager 2003, 2008). Darwin and the evolutionary synthesis drew on this tradition, and present-day demography may also find it fruitful. There remains, nonetheless, a particular interest in the central role that population acquired in Darwin's theory of natural

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[15] Serious shortcomings in some ambitious attempts to develop network hypotheses (e.g., Putnam 1993, 2000) arise from inattention to local network process and function (McLean 2007: 10-17).

selection, since it showed why both concepts of population are necessary, and how they may be combined to complement each other.

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